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Fecundity and Length at First Spawning of the Hawaiian Anchovy, or Nehu (*Stolephorus purpureus* Fowler) in Kaneohe Bay, Oahu[1]

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ABSTRACT: Fecundity, length at first spawning, and spawning seasonality of *Stolephorus purpureus* were deteımined by examining preserved ovarian eggs and fish captured throughout a 4-year period. Fecundity was estimated from the numbeı of eggs in the most advanced ovarian mode after it was determined that all these eggs hydrated and were spawned. Fecundity (Y) was related to fish weight (X) by the hyperbolic function, $Y = X/(0.0049–0.0033X)$. According to this relationship, a fish having a weight equal to the mean for the population contains 566 eggs/g of fish weight. Large variations in fecundity from year to year were attributed primarily to environmental factors whose influence on reproduction by *Stolephorus purpureus* has not been studied. Length frequencies of ovarian eggs were bimodal, but the smaller modes remained stationary regardless of the position of the larger modes. This was interpreted as evidence that individual fish spawned only once per year. From data on egg length versus fish length it was estimated that fish were first capable of spawning when 35 mm (standard length); the smallest fish observed to contain hydrated eggs was 37.8 mm. Captured fish containing hydrated eggs were rare, 1.1 percent of 1,735 adult females examined. Spawning occurred year around but the incidence was higher during the spring and summer than during the remainder of the year.

SUCCESS of the fishery for skipjack tuna (*Katsuwonus pelamis*) in Hawaii, which is the state's most important fish on the basis of tonnage landed and dollar value, depends largely on the use of a live bait fish (anchovy) known locally as nehu (*Stolephorus purpureus* Fowler). Under present fishing practices, the availability of nehu is an important factor limiting expansion of the skipjack fishery in Hawaii and the central Pacific area. Various aspects of the biology of nehu have been studied (Nakamura 1970); however, there are no published reports on their fecundity. This information is essential for estimating the inherent reproductive potential of the fish and, therefore, is an important consideration in managing the bait resource effectively.

The objective of this study was to further knowledge of the reproductive biology of nehu by determining their fecundity and the length of females at first spawning. We also examined spawning seasonality to compare our findings with earlier reports. Data were obtained by examining preserved specimens and their ovarian eggs.

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MATERIALS AND METHODS

Nehu were collected in Kaneohe Bay, southeastern Oahu. Collections were made at least monthly throughout 1967, 1968, 1969, and 1972 (exceptions: February and April 1967 and September, November, and December 1969). Fish were captured at night by lift net after being attracted to a light 1 m below the surface of the water which was up to 15 m deep; during the day they were caught by seining in shallow areas. Fish initially were preserved in 10-percent formalin; after 2 weeks they were rinsed in fresh water and stored in a 1:1 solution of propanol and water.

Data for determining egg length frequencies were obtained from collections chosen at random from all those available; every month of the year was represented at least once. Fish were deliberately selected to represent the entire range of lengths found within a collection, but otherwise selection was random. The selected individuals were measured (standard length) to the nearest 0.1 mm with dial calipers; their weights were calculated later from the relationship—weight = 6.53×10^{-6} length$^{3.109}$—reported for nehu by Struhsaker, Baldwin, and Murphy, in press. We determined fish weight indirectly because preservation in formalin generally affects length less than it does weight (Parker 1963). After fish were measured they were slit ventrally and examined for developing ovaries; males were discarded. The ovaries of females were removed, touched to absorbent paper, then weighed immediately to the nearest 0.1 mg on an analytical balance (Mettler, model H20T). Previous investigations established that eggs per gram of ovary were essentially the same for left and right ovaries of fishes closely related to nehu (MacGregor 1957, Peterson 1961). After determining that this was also true for nehu, we sampled only the left ovary. A subsample estimated to contain 250 eggs was removed, weighed as above, and placed on a slide in a drop of glycerin. After the subsample was teased into individual eggs, the long axis of each was measured to the nearest whole unit (130^{-1} mm) with an image-projecting device similar to one described by Mosher (1950). Frequency data were grouped by five-unit intervals to facilitate analysis. Fish in which the largest eggs were less than 0.14 mm long (the earliest stage of egg development at which the elongate form characteristic of mature nehu eggs was readily distinguishable) were replaced as necessary to assure that every month of the calendar year was represented by at least five fish.

In addition, all collections (113) were examined for fish about to spawn. Fish were selected at random from those judged to be the largest in the collection. Standard length was measured as above and the fish were slit ventrally to expose the gonads. If eggs were present, a small sample was removed with forceps from the posterior end of the left gonad, placed on a slide, and five of the largest eggs were measured to the nearest 0.1 mm with the micrometer of a binocular microscope. At least 15 females from each collection were treated in this manner except in cases where the collections contained fewer than 15 mature females. In all, 1,735 female fish were examined.

RESULTS

Fecundity

To estimate fecundity we had to identify those ovarian eggs that would be released at next spawning. In the case of a fish that spawns seasonally, eggs of all females in a population mature at approximately the same time and progressive development of the eggs can be followed by successive sampling. This approach does not work with nehu or other fishes that spawn year around because individuals at all stages of ovarian development are always present in the population.

Clark (1934) circumvented this problem in the case of the California sardine, *Sardinops caerulea*, by grouping fish she examined into arbitrary classes according to egg length of the most mature mode they contained. She then pooled egg length data from all fish assigned to the same class and plotted a series of egg length frequency diagrams that represented the classes. Arranged in order of increasing modal egg lengths, these plots provided a composite picture of ovarian development.

In the present study, using the procedure proposed by Clark, we grouped fish into 12 classes (each assigned a length of 10 image projector units) that together included all the

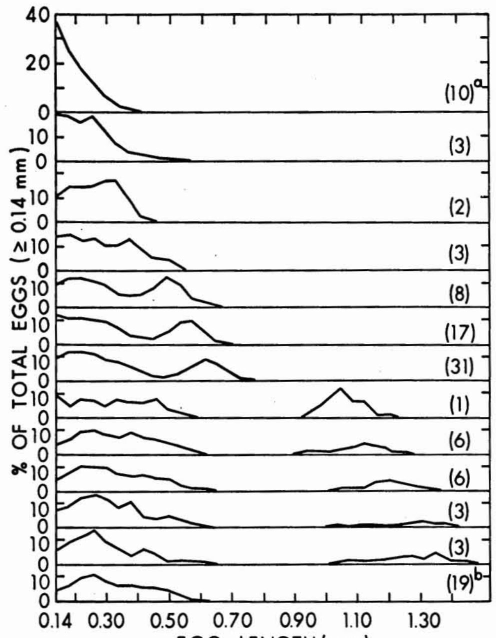

FIGURE 1. Length frequencies of ovarian eggs grouped by length of eggs forming the most advanced mode. *a*, Data were grouped into classes 10 units (0.088 mm) long. Numerals in parentheses indicate number of fish in each class; *b*, composite length frequency of unhydrated eggs from 19 fish found to contain hydrated eggs also.

TABLE 1

FREQUENCY DISTRIBUTION OF NUMBER OF HYDRATED EGGS/GRAM OF FISH WEIGHT

NUMBER OF EGGS	NUMBER OF FISH
0–100	3
101–200	4
201–300	5
301–400	5
401–500	1
501–600	1

Mean 248 (SE 31.1), Range 10–508

sizes of maturing eggs observed. Figure 1 shows the data from these fish plotted to depict the course of nehu egg maturation.

Initially all eggs formed a single mode at 0.14 mm, but as they developed beyond this point a second mode began to separate from the first. By the stage at which the advanced mode was at 0.49 mm, egg length frequency was clearly bimodal and remained so during growth of eggs in the larger mode to 0.60 mm. After the advanced mode reached this length there was an abrupt jump to a mode at 1.05 mm that consisted of hydrated eggs.[5] There were essentially no eggs intermediate between these two size ranges in any of the females examined.

We interpreted this situation to indicate that eggs attained a maximum length of approximately 0.60 mm before a final maturation stage of very short duration during which all eggs in the advanced mode rapidly hydrated to their final ovarian size and shortly thereafter were released. This interpretation is supported by the fact that 61.9 percent of the females that we surveyed in search of mature eggs contained eggs 0.60 mm or slightly more in length, but hydrated eggs were found in the ovaries of only 1.1 percent of all females examined. Furthermore, rapid hydration of eggs, resulting in increased size, typically is the final step in maturation of pelagic eggs such as those of nehu (Fulton 1898). Eggs of a closely related species, *Engraulis mordax*, were observed to hydrate and be released within hours while the fish were in captivity (Lasker, personal communication).

Based on the interpretation above, fecundity was estimated by counting the most advanced mode of unhydrated eggs. Direct counts of hydrated eggs were not used to determine fecundity because large variability in hydrated eggs/g of fish (Table 1) suggested that some individuals had spawned part of their eggs prior to capture or perhaps had lost them during the rough handling attending capture. There was no way to tell which fish had released eggs nor what percentage of their hydrated eggs they still retained when they were collected. Figure 2 shows the relationship between fecundity, which often increases with fish size (Blaxter 1969), and total weight for 41 nehu. These fish were selected from those whose eggs were measured and counted because the data on egg length frequency of each one exhibited a well-defined mode of advanced eggs.

Fecundity-length and fecundity-weight data

[5] Hydration occurs during the final stages of egg maturation in some marine teleosts. Fluids of lower specific gravity than seawater are secreted into the egg by granular cells of the follicle causing a three- to four-fold increase in volume that assures that the eggs will float when they are released (Smith 1957).

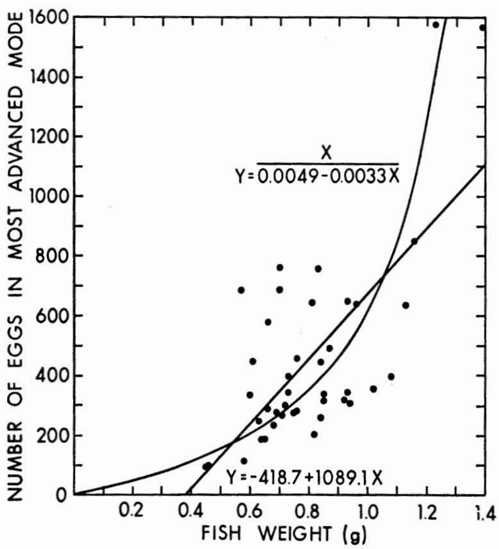

FIGURE 2. Fecundity-weight relationship for 41 fish.

for fish were fitted by the method of least squares to seven general equations commonly found to describe biological relationships. The equations are: $Y = A + BX$, $Y = Ae^{BX}$, $Y = AX^B$, $Y = A+(B/X)$, $Y = 1/(A+BX)$, $Y = X/(A+BX)$, and $Y = A+B \log X$. Data fitted best to the hyperbolic function, ($Y = X/0.0049-0.0033X$), with weight as the independent variable ($r = .720$, $P < 0.01$). MacGregor (1957) also found a better correlation between fecundity and weight than between fecundity and length for *Sardinops caerulea*, a species related to nehu.

Figure 2 suggests that the linear equation, $Y = -418.7+1089.1X$, describes the data as well as the curvilinear one except at the upper extreme of fish size ($r = .683$, $P < 0.01$). Statistical test of the difference between r values for these two functions by the method of Steel and Torrie (1960) indicated that the correlations are not significantly different ($z = 0.32$, probability of a greater z occurring by chance $= 0.75$). Because of this finding and the fact that the majority of the population is within the range described equally well by either equation, we used the linear one because of its greater simplicity. According to this equation, fecundity of a hypothetical fish having a weight equal to the mean weight of the population was 566 eggs/g of fish weight. This figure is consonant with those reported for other engraulids; e.g., *Cetengraulis mysticetus*, 836 eggs/g of fish weight (Peterson 1961); *Engraulis mordax*, 574 eggs/g of fish weight (MacGregor 1968).

Theoretically, fecundity should be a cubic function of length because ovary volume is a determinant of the number of eggs that can be contained. Many workers have reported this relationship to be true for the fishes they studied (Blaxter 1969); however, MacGregor (1968) and Peterson (1961) found that a linear relationship to either length or weight described fecundity of *Engraulis mordax* and *Cetengraulis mysticetus* as well as curvilinear functions. MacGregor suggested that the short range of lengths of spawners and wide variation in fecundity of individuals the same length obscured the true curvilinear nature of the fecundity-length relationship.

We cannot explain conclusively the marked variation in egg production by fish within the same size class; however, some of the variability probably is attributable to differences in environmental conditions among years during which the collections were made. Mean fecundities for 1967, 1968, 1969, and 1972 were 503, 463, 598, and 738 eggs/g of fish, respectively. Analysis of variance of the means is not significant ($F = 1.08$) and no mean was significantly different from the others (Duncan's new multiple range test; Kramer 1956); however, large variation within years probably masked the effects of whatever environmental differences existed among years. It has been shown that such differences can influence fecundity under natural (see Blaxter 1969) and experimental conditions (Scott 1962, Hester 1964).

Another factor which probably contributed to the variation in nehu fecundity was technician error. The method used to determine fecundity depended critically on exact weights of ovaries and ovarian subsamples. Careful and consistent technique was necessary to make the weighings precisely because of the rapid evaporation of the alcohol preservative during the operation. Because circumstances dictated that three different technicians take part in this study, an unknown amount of variation was introduced into the data by differences in the way they performed this delicate step.

Frequency of Spawning

The number of times an individual spawns per year is as important in estimating fecundity as number of eggs released at each spawning. For an individual nehu, eggs spawned per year probably is synonymous with total eggs released since few of these fish live for a second year (Bachman 1963). There was no direct evidence of multiple spawning, such as eggs or larvae from a previous spawning undergoing resorption in the ovary at the same time that another batch of eggs was about to be released (MacGregor 1970). However, the length-frequency distribution of nehu eggs as they matured to the point of hydration was bimodal; some authors have considered this to be presumptive evidence of multiple spawning in other fishes (Clark 1934, MacGregor 1957).

Other indications argue against more than one spawning by nehu. Figure 1 shows that the secondary mode of eggs was at approximately the same length regardless of the position of the advanced mode of unhydrated eggs. This observation suggests that eggs in the secondary mode did not increase in size simultaneously with those of the advanced mode as would be expected if the smaller ones also were to mature for subsequent release. Although length-frequency diagrams for the smaller eggs of some of the fish that contained hydrated eggs suggest that a second group of eggs was beginning to separate from the others, the appearance of bimodality may have been an artifact resulting from the small number of individuals in each length category. When length-frequency data for the smaller eggs from the 19 fish that also contained hydrated eggs were pooled, the plot was unimodal (Figure 1). This fact supports the possibility that bimodality of these smaller eggs was apparent rather than real. Because eggs forming the smaller mode did not grow while those in the advanced mode proceeded to maturity, it is doubtful that the second group developed to spawning. Based on this indirect evidence we tentatively conclude that individual nehu spawn only once per year. Howard and Landa (1958) concluded on similar grounds that the anchoveta, *Cetengraulis mysticetus*, spawns once per year and resorbs any developing eggs that have not been released.

Length at First Spawning

The smallest nehu found to contain hydrated eggs was 37.8 mm long; however, there is evidence that these fish are capable of spawning when smaller than this. Figure 3 shows the relationship between fish length and length of eggs forming the most advanced mode. The figure comprises data from 100 fish selected at random from collections representing all months of the calendar, but various years. (An exception was deliberate selection of some individuals from the lower end of the size range to obtain additional data from fish whose largest eggs were smaller than 0.14 mm but still large enough to measure individually.) Eggs of fish 30 to 35 mm long consistently were within the range 0.03 to 0.08 mm, but egg length of nehu 35 to 36 mm abruptly increased to an upper limit of approximately 0.62 mm. We interpreted this jump in egg length to a size typical of eggs just prior to hydration as an indication that nehu first become capable of spawning when 35 to 36 mm. The time required for nehu to attain this length is not known. Yamashita (1951) estimated that they reach adult length (30 mm) 6 to 7 weeks after hatching, but there is no information on how long it takes them to grow an additional 5 to 6 mm and develop mature eggs.

Not all females 35 mm or more in length contained eggs in late stages of development. A number of large nehu (40 to 53 mm) plotted in Figure 3 had their most advanced egg modes in the range 0.20 to 0.45 mm, which corresponds to the range that includes most modes of the smaller eggs from fish that contained hydrated eggs also (see Figure 1). A reasonable explanation for the presence of these individuals is that they were fish that had spawned recently and at capture contained only eggs of the secondary mode.

We also observed females longer than the minimum length for spawning that did not contain significantly developed eggs; these fish indicate that reaching a threshold length was not the only prerequisite for egg maturation. Seasonality of peak spawning (see following section) suggests that environmental factors were involved also. Tester (1955) proposed a possible dependence on water temperature but

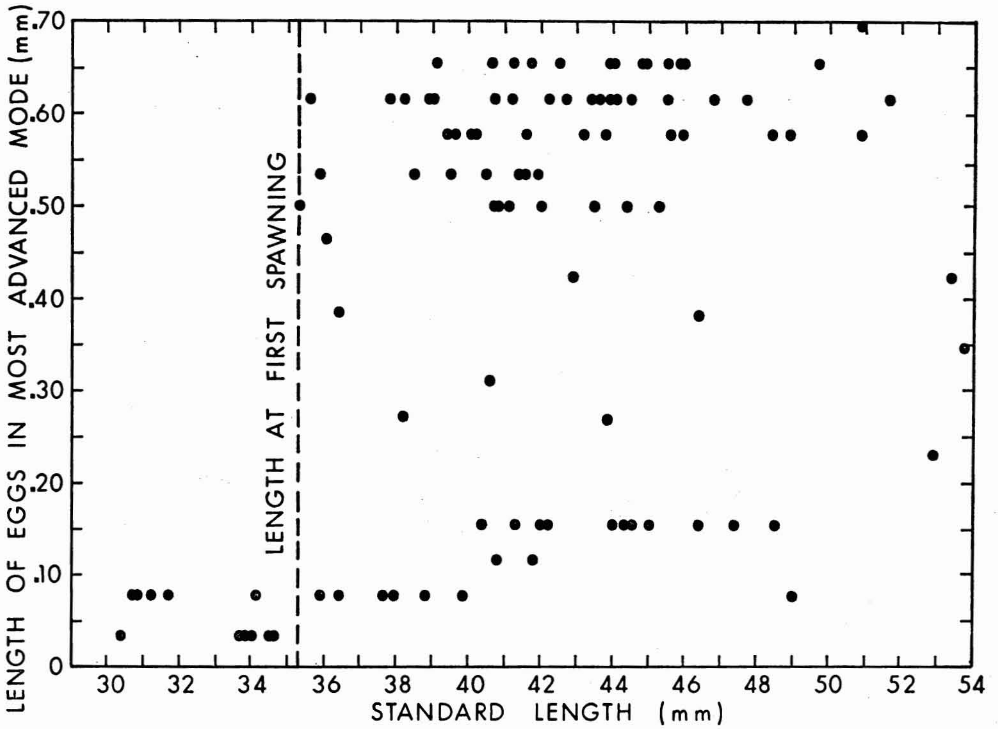

FIGURE 3. Relationship between standard length of fish and length of eggs forming the most advanced mode. The estimated length of nehu at first spawning is indicated.

was not able to demonstrate this relationship conclusively. It is our proposition that a fish that reaches threshold size when environmental factors are not favorable continues to grow but does not develop mature eggs until conditions improve. Conversely, under favorable circumstances, a fish develops and releases eggs as soon as she has reached the necessary size. If we are correct, relatively large fish containing eggs that have not begun to mature would probably occur when spawning conditions are not favorable, and the incidence of spawners that have recently attained threshold size would be highest during favorable periods.

There is evidence to support both ideas. Fourteen of the 100 nehu plotted in Figure 3 contained only immature eggs (0.16 mm or less), even though the fish were 40 mm or more in length. Ten of these were from collections made during the winter and fall quarters when the incidence of spawning was lower—and, hence, conditions presumably were less favorable—than during the other half of the year (see following section). A test of independence (Sokal and Rohlf 1969) indicated that the tendency for these large nehu with immature eggs to have occurred more frequently during the fall-winter half of the year approached statistical significance ($G = 3.64 < \chi^2_{.05} = 3.84$).

In support of the other prediction, i.e., that small but mature fish would be more likely to occur when conditions are favorable for spawning, Figure 4 shows length = frequency plots by quarter for those females considered mature on the basis of containing eggs 0.6 mm or larger. Although mean fish lengths remained essentially constant from quarter to quarter, percentages of mature fish within the first five millimeters (35 to 40 mm) beyond minimum spawning size were 6.2, 16.6, 6.4, and 1.7 percent for quarters 1 through 4, respectively. A test of independence indicated that the incidence of small, mature fish was associated with quarter to a highly significant extent ($G = 27.92 > \chi^2_{.01} = 11.34$); simultaneous test pro-

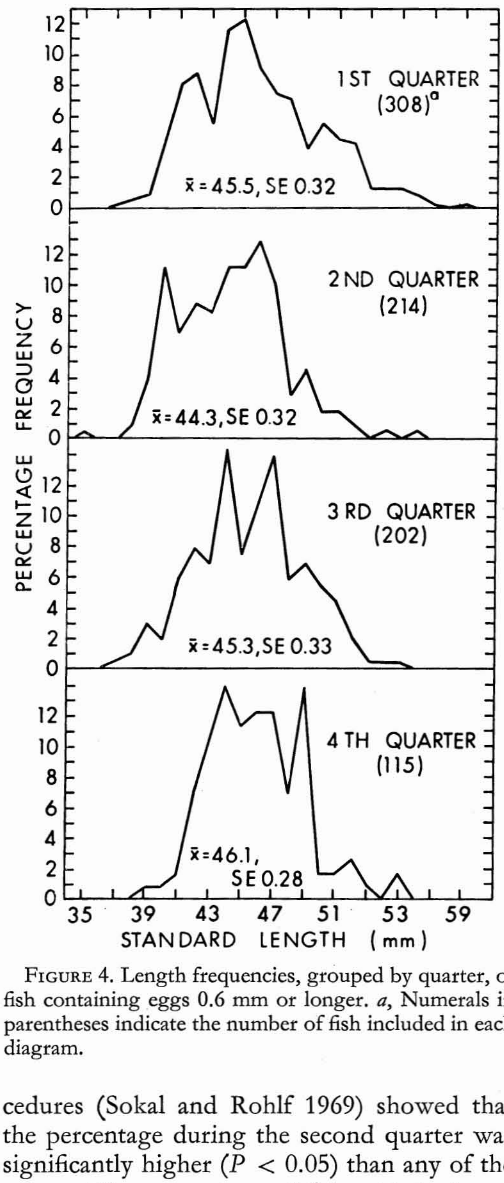

FIGURE 4. Length frequencies, grouped by quarter, of fish containing eggs 0.6 mm or longer. *a*, Numerals in parentheses indicate the number of fish included in each diagram.

cedures (Sokal and Rohlf 1969) showed that the percentage during the second quarter was significantly higher ($P < 0.05$) than any of the others. The percentage of fish with hydrated eggs was also highest during the second quarter, which suggests that conditions were conducive to spawning at that time (see following section).

Temporal and Spatial Distribution of Spawning

We found fish containing hydrated eggs in collections from every quarter of the year except the last. Other data (Brogan, unpublished) on nehu captured in Kaneohe Bay during the last quarter of 1967 indicated that fish with hydrated eggs were present at that time. Based on this evidence, we concur with Tester (1955) that nehu spawn year around in Kaneohe Bay.

Determining the quantitative distribution of spawning throughout the year was more difficult. Based on the percentage of females that contained hydrated eggs, spawning frequencies were 0.77, 2.36, 1.90, and 0.74 percent for the 1st through 4th quarters, respectively. Spawning activity was independent of quarter according to the results of an independence test ($G = 6.18 < \chi^2_{.05} = 7.81$). However, by pooling data from quarters 1 and 4 to form one class and from quarters 2 and 3 to form another, we found that 2.02 percent of the females were in spawning condition during the spring-summer period and 0.75 percent during the winter-fall period. A test of the data arranged in this manner indicated that the dependence of spawning on time of year is significant ($G = 5.67 > \chi^2_{.05} = 3.84$). We conclude that nehu spawn more in the spring and summer than during the winter-fall portion of the year, which is in agreement with Tester's findings (1955).

Frequency of nehu containing hydrated eggs in our collections may not be a reliable indication of spawning activity because the rarity of ripe females among captured fish, which appears to be characteristic of nehu and related species (Clark 1934, Howard and Landa 1958), causes sampling difficulties that can lead the investigator to erroneous conclusions. For instance, two collections from a total of 113 yielded 12 of the 19 nehu found with hydrated eggs. Apparent high frequency of spawning in these two samples probably was an artifact resulting from clumped distribution of nehu with hydrated eggs. A goodness-of-fit test (Sokal and Rohlf 1969) verified that the occurrence of such fish in the population did not follow the Poisson distribution describing rare, random events ($\chi^2 = 36.70 > \chi^2_{.01} = 18.48$); furthermore the ratio of population variance to mean (4.98) was significantly ($P < 0.05$) greater than 1, thus substantiating the theory that nehu with hydrated eggs associated more than chance would predict (Andrewartha and Birch 1954:

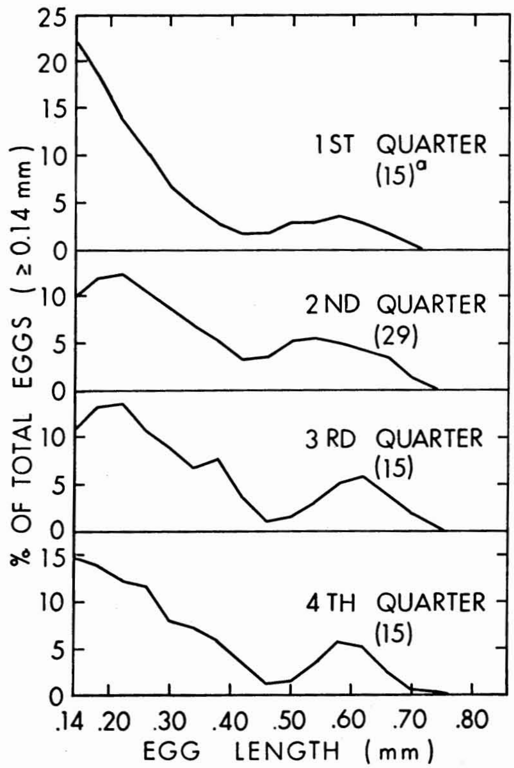

FIGURE 5. Mean length frequencies, grouped by quarter, of eggs from five or more fish collected in each month. *a*, Numerals in parentheses indicate the number of fish from which data were taken for pooling.

557–647). It is likely that this clumping reflects a tendency for spawners to group in preparation for reproduction. Although spawning behavior of nehu has not been reported, ripe individuals of species related to nehu are known to aggregate for spawning into small subgroups within the larger school (Breder and Rosen 1966: 605–617).

The data also provided indirect evidence on the temporal distribution of reproduction. Figure 1 shows that nehu with the most advanced mode of eggs at approximately 0.6 mm had matured to a point just short of egg hydration. The percentage of females having their advanced mode at this stage during a given period should provide an index of spawning activity at that time. These percentages for the 1st through 4th quarters were 33.3, 34.5, 66.7, and 40.0, respectively. A test of independence indicated that the individual frequencies were not significantly associated with time of year ($G = 4.88 < \chi^2_{.05} = 7.81$), nor were the pooled frequencies for winter-fall and spring-summer ($G = 0.13 < \chi^2_{.05} = 3.84$). However, the association of nearly mature fish with the 3rd quarter was significant ($G = 6.09 > \chi^2_{.05} = 3.84$); such relationships did not exist for the other quarters when tested individually. This evidence suggesting a spawning peak during the 3rd quarter is consistent with Tester's data (1955) showing a maximum number of eggs in the water column at this time of year.

Another indication of spawning seasonality was obtained from the relationship between quarter and egg length. Five or more fish were selected at random to represent each month of the year; their mean egg length frequencies are plotted by quarters in Figure 5. In all quarters a mode was present at the maximum size for nonhydrated eggs that is consistent with our previous observation and that of Tester (1955) that spawning occurred year around. Throughout the year there was a preponderance of small eggs, but the dominance of these was greater during the 1st and 4th quarters than during the 2nd and 3rd. These data suggest that there was less spawning during the winter-fall half of the year than during the spring-summer half. This also is in agreement with our data on frequency of nehu with hydrated eggs, and Tester's report (1955) that spawning was maximum in summer and minimum in winter.

Time and location of capture of nehu with hydrated eggs were as expected on the basis of previous reports. All such individuals were from collections taken at night between 2100 and 2300 hours. This is consistent with our tentative conclusion that hydration of nehu eggs occurs very rapidly, immediately before release, and with Tester's report (1955) that nehu spawning is at its peak from 2200 to 2400 hours. Four of the five collections that contained fish with hydrated eggs were made in water 12 to 15 m deep; the remaining one was taken in 2 to 3 m of water. Tester (1955) reported that he found greatest abundance of nehu eggs in water 12 to 15 m deep.

DISCUSSION

Our study clearly reveals several unsolved problems. For instance, what factors are responsible for the wide variation in fecundity of females of identical size? Some of the variation can be attributed to sampling errors, but environmental factors likely are responsible for most of it. The influence of environmental factors on nehu reproduction has not been investigated yet. We have no conclusive evidence on the number of times a female spawns per year, nor do we know whether or not an individual survives to spawn during more than 1 year. Growth rate of adult nehu is not known precisely; therefore, even though we now have information on the length of females at first spawning, we do not know how long it takes them to reach this size and mature their eggs.

The information available at present indicates that the reproductive pattern that best fits nehu is characterized by a fish that matures within a few months and then spawns several hundred eggs but probably does not live long enough to spawn again because of a very high mortality rate, presumably from predation.

LITERATURE CITED

ANDREWARTHA, H. G., and L. C. BIRCH. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago. xv+ 782 pp.

BACHMAN, R. 1963. Fluctuations and trends in the abundance of nehu (*Stolephorus purpureus* Fowler) as determined from catch statistics. M.S. Thesis. University of Hawaii, Honolulu. 100 pp.

BLAXTER, J. H. S. 1969. Development: eggs and larvae. Pages 177–252 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology. Vol. III. Academic Press, New York.

BREDER, C. M., Jr., and D. E. ROSEN. 1966. Modes of reproduction in fishes. Natural History Press, Garden City, New York. xv+941 pp.

CLARK, F. N. 1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. California Div. Fish & Game, Fish Bull., Sacramento 42. 49 pp.

FULTON, T. W. 1898. II. On the growth and maturation of the ovarian eggs of teleostean fishes. Sixteenth annual report of the Fishery Board of Scotland. Part III: 88–124.

HESTER, F. J. 1964. Effects of food supply on fecundity in the female guppy, *Lebistes reticulatus* (Peters). J. Fish. Res. Bd. Can. 21: 757–764.

HOWARD, G. V., and A. LANDA. 1958. A study of the age, growth, sexual maturity, and spawning of the anchoveta (*Cetengraulis mysticetus*) in the Gulf of Panama. Bull. inter-Amer. trop. Tuna commn. 2(9): 391–467.

KRAMER, C. Y. 1956. Extension of multiple range tests to group means with unequal numbers of replications. Biometrics 12: 307–310.

MACGREGOR, J. S. 1957. Fecundity of the Pacific sardine (*Sardinops caerulea*). Fish. Bull. U.S. 121, vol. 57: 427–449.

———. 1968. Fecundity of the northern anchovy, *Engraulis mordax* Girard. California Fish and Game 54(4): 281–288.

———. 1970. Fecundity, multiple spawning, and description of the gonads in *Sebastodes*. Spec. sci. Rep. U.S. Fish Wildl. Serv. 596. 12 pp.

MOSHER, K. H. 1950. Description of a projection device for use in age determination from fish scales. Fish. Bull. U.S. 54, vol. 51: 405–407.

NAKAMURA, E. L. 1970. Synopsis of biological data on Hawaiian species of *Stolephorus*. Pages 425–446 *in* J. C. Marr, ed. The Kuroshio: a symposium on the Japan Current. East-West Center Press, Honolulu. 614 pp.

PARKER, R. R. 1963. Effects of formalin on length and weight of fishes. J. Fish. Res. Bd. Can. 20: 1441–1455.

PETERSON, C. L. 1961. Fecundity of the anchoveta (*Cetengraulis mysticetus*) in the Gulf of Panama. Bull. inter-Amer. trop. Tuna Commn. 6(2): 55–68.

SCOTT, D. P. 1962. Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. J. Fish. Res. Bd. Can. 19: 715–730.

SMITH, S. 1957. Early development and hatching. Pages 323–359 *in* M. E. Brown, ed. The physiology of fishes. Vol. 1. Academic Press, New York.

SOKAL, R. R., and F. J. ROHLF. 1969. Biometry. W. H. Freeman Co., San Francisco. 776 pp.

STEEL, R. G. D., and J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., New York. 481 pp.

STRUHSAKER, J. W., W. J. BALDWIN, and G. I. MURPHY. In press. Environmental factors affecting stress and mortality of the Hawaiian anchovy (*Stolephorus purpureus*) in captivity. Univ. of Hawaii, Sea Grant Tech. Rep.

TESTER, A. L. 1955. Variation in egg and larva production of the anchovy, *Stolephorus purpureus* Fowler, in Kaneohe Bay, Oahu, during 1950–1952. Pacif. Sci. 9(1): 31–41.

YAMASHITA, D. T. 1951. The embryological and larval development of the nehu, an engraulid bait fish of the Hawaiian islands. M.S. Thesis. University of Hawaii, Honolulu. 64 pp.